How Art and Neuroscience Fell for Each Other

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This chapter will provide a brief tour of what neuroscience can learn from art, of what neuroscience can tell us about our relationship with art, and, on the way, a glimpse of what art and neuroscience can teach us about our humanity. The first part will remind us that, because humans are produced by evolution, neuroscience and art are deeply interlaced. The second part will focus on the effects of art observation on our brain activity. Lastly, the third part will emphasize how our mind-body interacts with artworks.

Did we, humans, evolve for art?

Art, without a doubt, is one of humanity's greatest achievements. It could even be what distinguishes us, humans, within the animal reign. However, this should not deny the role of biology, neither in the way art is created, nor in the way it is received. Geoffrey Miller ((2000), also cited in Pinker (2002)), observing the charming and sophisticated nests built by male birds of certain species, writes:

If you could interview a male Satin Bowerbird for Artforum magazine, he might say something like "I find this implacable urge for self-expression, for playing with color and form for their own sake, quite inexplicable. I cannot remember when I first developed this raging thirst to present richly saturated color-fields within a monumental yet minimalist stage-set, but I feel connected to something beyond myself when I indulge these passions. When I see a beautiful orchid high in a tree, I simply must have it for my own. When I see a single shell out of place in my creation, I must put it right. Birds-of-paradise may grow lovely feathers, but there is no aesthetic mind at work there, only a body's brute instinct. It is a happy coincidence that females sometimes come to my gallery openings and appreciate my work, but it would be an insult to suggest that I create in order to procreate. We live in a post-Freudian, post-modernist era in which crude sexual meta-narratives are no longer credible as explanations of our artistic impulses".

Fortunately, bowerbirds cannot talk, so we are free to use sexual selection to explain their work, without them begging to differ.

By placing a caricature of an artist's speech into the Bowerbird's beak, Miller favors an interpretation that gives a large role to sexual selection in the production of art. This is not the only interpretation based on evolution theories. In general, such interpretations try to find what would be attractive to us as a species. For instance, a list of universal principles of art has been proposed by Ramachandran (2005). Among them, "Peak shift" was inspired by Tingbergen's experiments. As soon as a herring-gull chick hatches, it starts pecking at the red spot on the long yellow beak of its mother to beg for food. Based on this observation, Tingbergen showed that the chicks displayed a strong preference for long yellow sticks with three red stripes, actually larger than for a real beak, as if the sticks were "superbeak". Ramachandran proposes than human artists, through trial, error, and intuition, similarly discover the "figural primitives of our perceptual grammar" and exaggerate them in their artworks. For instance, we may find Picasso's paintings appealing because our brains' face-recognition system (which evolved to find faces attractive) becomes "hyperactivated" by the simultaneous presentation of different views of the same face.

This chapter will not defend any one theory about the purpose of art. Rather, neuroscientific studies will be surveyed to bring forth insight on the neurophysiological mechanisms by which art moves us (both in terms of physical and of emotional movements).

Does our brain enjoy art?

Neuroaesthetics is a recent field of research, where most studies are mainly directed towards characterizing the cortical and subcortical activations associated with viewing artworks, intrinsically beautiful objects, or objects we personally find beautiful (to what extent art and beauty do overlap is often beyond most neuroaesthetics studies).

Unsurprisingly, the neuroimaging results on art perception show great heterogeneity. Indeed, there is huge variability on types of artworks and as many ways to formulate a scientific question to answer the fundamental question: "how do we perceive art?" Nevertheless, some brain areas have been repeatedly coupled with art perception. Studies with functional magnetic resonance (fMRI)[1], electroencephalography (EEG)[2], and transcranial magnetic stimulation (TMS)[3] revealed that areas that have been previously associated to the reward system (e.g., orbitofrontal cortex), to emotional processing (e.g., amygdala, insula) or areas related to high-level cognitive processes (e.g., prefrontal cortex), are activated during aesthetics experience (Brown et al., 2011; Di Dio and Gallese, 2009; Di Dio et al., 2007; Ishizu and Zeki, 2011). Interestingly, in line with theories of embodied cognition, several studies revealed that artworks also impact parietal and sensorimotor systems.

Based on our largely shared taste for beauty, some studies focused on intrinsic, objective, characteristics of artworks that make us admire them, and on exploring how those characteristics impact neural activity. Di Dio et al. (2007) invited participants in an fMRI scanner to observe, as if they were in a museum, images of classical (e.g., Doryphoros by Polykleitos) and Renaissance sculptures, as well as versions of these sculptures with modified proportions. When no explicit behavioral response was requested (participants were invited to make an aesthetic judgment later, outside the scanner) a greater activation was shown for the original than for distorted sculptures

[1] Functional magnetic resonance imaging (fMRI) is a neuroimaging technique that supposedly measures brain activity by detecting changes associated with oxygenated and deoxygenated blood flow.

[2] Electroencephalography (EEG) is neuroimaging technique that records electrical activity of the brain. When focusing on the spectral content of recorded signals, EEG typically evaluates neural oscillations or "brain waves".

[3] Transcranial magnetic stimulation (TMS) is a noninvasive neuroimaging technique used to stimulate small regions of the brain. Reversibly disturbing the ongoing neural activity, it is useful to evaluate the causal involvement of specific brain areas.

in the insula: the activation perhaps reflected the pleasure evoked from the original sculptures' perfect proportions. Is the insula playing the role of an art-detector? In another study, however, different areas were shown to be important. Lutz et al. (2013) examined the difference between perceiving human bodies in artworks (from ancient renaissance artists as Peter Paul Rubens to contemporary ones as Ernst Ludwig Kirchner) and in non-artistic media. Compared to non-artistic photographs, artistic paintings evoked more activity in the right parietal cortex and the bilateral extrastriate cortex, stressing upon an enhanced processing of visuo-spatial information for artistic stimuli. These two studies also showed that the original works were more appreciated than their modified versions, or than the non-artistic media. The above-mentioned activations could thus facilitate the development of a positive aesthetic judgment.

Another approach emphasized subjective appreciation of art, and focused on individual preference and its neurophysiological correlates. A meta-analysis of 93 neuroimaging studies asking participants to make explicit aesthetic judgments revealed the importance of the right anterior insular cortex for perceiving beauty in four different perceptual modalities (Brown *et al.*, 2011). Instead of working as an art-detector, could the insula serve to perceive beauty? According to another study, however, this role might be rather subtended by the orbitofrontal cortex. Ishizu & Zeki (2011), selecting artworks from both western and oriental cultures, explored the common substrate of beauty perception in visual (painting) and auditory (music) modalities. The results supported their theory, which relates the phenomenological experience of beauty to the activation of the orbitofrontal cortex. In other words, objects that are commonly considered beautiful might have universal properties, but the extent of their appreciation by an individual depends primarily on the activity within the orbitofrontal cortex. Nevertheless, confounding factors might have artificially increased the orbitofrontal cortex' role in beauty perception. Activity within this brain area seems to be also influenced by the "status" of the artistic object: when participants believed that an artwork originates from a museum, the median orbitofrontal cortex showed larger activation than when they believed it has been generated by a computer (Kirk et al., 2009).

In any case, viewing artworks obviously engages multiple brain networks. Calvo-Merino et al. (2010) identified two potential pathways for the aesthetic treatment of static ballet postures images. The first path goes through the extratriate body area, believed to house local representation of body parts, whereas the second one goes through the ventral premotor cortex, believed to process configural representation of complete body posture. Using TMS to disturb the balance between these two areas modulates sensitivity to aesthetic ballet postures images. However, our perception of art is not only determined by the intrinsic features of artworks. Context, emotional state, individual interest, background knowledge, familiarity with the works, etc., have strong influences. Cupchik et al. (2009) invited participants to approach social (nude, group portrait) and non-social (still-life, landscape) figurative soft-edge or hard-edge paintings either in an objective and detached way, in search of narrative information or, alternatively, to get personally involved and to focus on emotions and composition. Some brain areas revealed style-dependent activation; e.g., the upper left parietal lobe, which was more activated for soft-edge than for hard-edge paintings, may facilitate the visual-spatial exploration of more challenging visual stimuli. Other brain areas revealed context-dependent activation; e.g., the left prefrontal lateral cortex, which increased its activity when artworks were approached with an aesthetic angle, may reflect higher personal introspection.

Finally, appreciating artworks may be related to feeling whatever the artists try to convey. For instance, does motion depiction induce greater activation in the brain areas specialized in movement detection (MT+, MT/V5)? Are such activations related to the appreciation of the artwork? Kim and Blake (2007) demonstrated with fMRI that such areas were more activated for abstract paintings with implied motion (e.g. Marcel Duchamp, ‘Nude Descending a Staircase No 2’) than for abstract paintings with little motion impression (Fig. 1B). This was found only in observers with prior experience to those kinds of paintings. Yet, in another study, these areas seemed to be important in art-naïve participants: applying TMS on them decreased the sense of movement they had in front of the paintings, but also decreased their appreciation of abstract (but not representational) artworks (Fig. 1C-D) (Cattaneo et al., 2015). Thus, the appreciation of abstract artworks could be related to feeling what is both there and not there: in the last example, movements in a static painting.

Does our mind/body play with artwork?

As mentioned earlier, many artists consciously or intuitively discovered how our brain works. We perceive and experience what they intended us to see and feel. Artists rely for instance on their explicit or implicit knowledge of our visual system in order for them to play with our perception. Indeed, whereas certain physics laws are unconsciously integrated in our brains, allowing us to unambiguously understand the world, some physical transgressions can be ignored with impunity. A shadow, for example, must be darker than its immediate surroundings; if not, it will not be properly interpreted. On the contrary, it can take various fanciful colors or shapes without shocking us, like in a painting from Fra Carnevale (Cavanagh, 2005). We can be just as impressed with the artists’ virtuosity in reproducing the real world as surprised by their ability to take liberty. Sometimes, neuroscience later formally demonstrates (or still has to) the laws of our perceptual systems that artists empirically illustrate.

Through centuries, artists learned to master the depiction of space and then, to go beyond the reproduction of reality. To enjoy a full 3D perception, our brain combines binocular disparity cues (the slight offset between the two images received by the eyes), size cues (the fact that farther objects appear smaller), perspective cues (e.g., the fact that parallel lines get closer when going farther), as well as a priori knowledge (e.g., a face is convex, not concave; close objects are usually in the lower-visual field). Even if not all are present at the same time, these clues help us to quickly navigate depth. An artful transgression of any of these laws will create fascinating artifacts. Such transgression can even create powerful illusions. If you look straight ahead to the sculpture House 1 by Roy Lichtenstein, you simply see a house. Turn around the house and you will quickly realize that it is not convex, like a real house, but instead concave. In addition, this “house” is quirky; there is not a single right angle! The edge wall that seemed pointed towards you is actually farther than the sidewalls. You were misled by the larger size of this edge and your prior general knowledge about houses. These spatial cues are so strong that when you return to your original position, you cannot prevent yourself from seeing, once again, an almost normal house even though you may be more sensitive to small inconsistencies, e.g., to how the house reposes on the ground.

Such illusions suggest that our perceptual system uses cognitive shortcuts to quickly, and often correctly, perceive the world. The most plausible interpretation is imposed on us and can never be entirely overthrown. At the opposite extreme, when the sum of available evidence is ambiguous and several interpretations are equally plausible, a phenomenon of multistability arises. Only one interpretation is imposed on us at a time, but our brain ends up questioning it and another interpretation takes over, and so on. Many artists created multistable arworks (e.g., MC Escher, Sandro Del-Prete, Jos De Mey). Because the physical world and the content of our percepts often do not match, illusion and multistable artworks are providing a unique source of inspiration for neuroscientists exploring not only our visual system, but also our perceptual consciousness. Of course, listing all the types of inspiration we could get from art would be endless. Illusions and other visual phenomena might as well trigger, simultaneously, a real-world sensation and a supernatural sensation (see e.g., the painted murals by José Clemente Orozco in Guadalajara, Mexico).

Besides these fascinating aspects, how could these artistic treatments participate in our aesthetic experience? One hypothesis is that, our experience of art is embodied: through our spatio-motor system, our body will truly interact with artworks. Let us first go back to our visual system. Visual information does not come to us: we have to actively look for it, and bring the objects of interest at the center of our retina. The phenomenological experience of looking for information in real life is entirely different from the experience of being still and receiving information, like in most non-motor visual perception experiments (Wurtz, 2008; Wurtz et al., 2011). Moreover, there is a permanent and complex interaction between the *physical* world, the *movements* made to explore it and the *perception* of it. In the case of depth, for instance, physical cues might participate in both the percept elaboration and the eye movements preparation (Ziegler and Hess, 1997). Additionally, efferent copies of motor signals contribute to percept elaboration (Priot et al., 2012). Conversely, in the presence of an illusory percept, eye movements are sometimes triggered according to the physical stimulus (Wismeijer et al., 2008) and sometimes according to the illusory percept (Sheliga and Miles, 2003).

The way our eyes explore artworks might contribute to how we interpret them. For example, the sensation of motion when viewing mathematically-generated Op Art seems to emerge from an unstable eye motor behavior made of many small saccades (Zanker et al., 2003; Zanker and Walker, 2004). The perception of space in Renaissance artworks from Piero della Francesca, containing strong depicted perspective, seems to come from two motor aspects: first, an active exploration and repeated fixations over areas of the paintings that are important for spatial composition, even when no figurative elements are depicted; second, gaze instability in depth, i.e., small vergence movements, even if the painting is 2D (Kapoula et al., 2009).

This instability in depth is not limited to the eye movement behavior. Abstract paintings from Maria Helena Vieira da Silva containing depth elements cause greater postural instability than modified versions of these paintings, which eliminate those depth cues (Kapoula et al., 2011). Representation of movements and instability also induce mild postural instability in observers. Nather et al. (2010) showed significantly greater body sways when participants observed a picture of a Degas' sculpture of a dancing ballerina than of a static ballerina, demonstrating that images of body movement internally generate unconscious body oscillations (Fig. 1E). A complex interaction between artworks, eye movements, and postural stability was demonstrated in two studies. One used reproductions of Op Art artworks from Riley and from Kitaoka (Fig. 1F) (Kapoula et al., 2015), and another one was conducted in a museum in front of the monumental Richard Serra's Promenade sculpture (Kapoula et al., 2014). These experiments illustrate how artworks, excelling in representing depth, movement and instability, are able to physically impact us.

Furthermore, we would be particularly sensitive to artistic stimuli inducing some kind of motor resonance. Obviously, dance is particularly suited to induce such physiological response. For example, some portions of the occipito-temporal and parietal areas of the network dedicated to the observation of actions would be especially active when we evaluate movements as both pleasing and difficult to reproduce (Cross et al., 2011). Similarly, bilateral sensorimotor cortex would be particularly activated when observing movements that are on average highly appreciated (Calvo-Merino et al., 2008). However, real movements are not the only ones able to activate the parietal and sensorimotor network. In paintings, not only figurative content but also visible traces of the creative artists' gesture can cause space and movement sensations that add to the aesthetic experience. For example, an EEG study revealed that observing artworks by Lucio Fontana made of cuts on canvas evoked modifications of brain oscillations similar to those observed during motor preparation. Modified versions of these works containing drawn lines instead of the cuts did not evoke such modification (Umilta et al., 2012). Thus, the EEG allows us to demonstrate a true motor preparation while observing some artworks. Entering in resonance with the creative gesture: is there a more beautiful way to appreciate art?

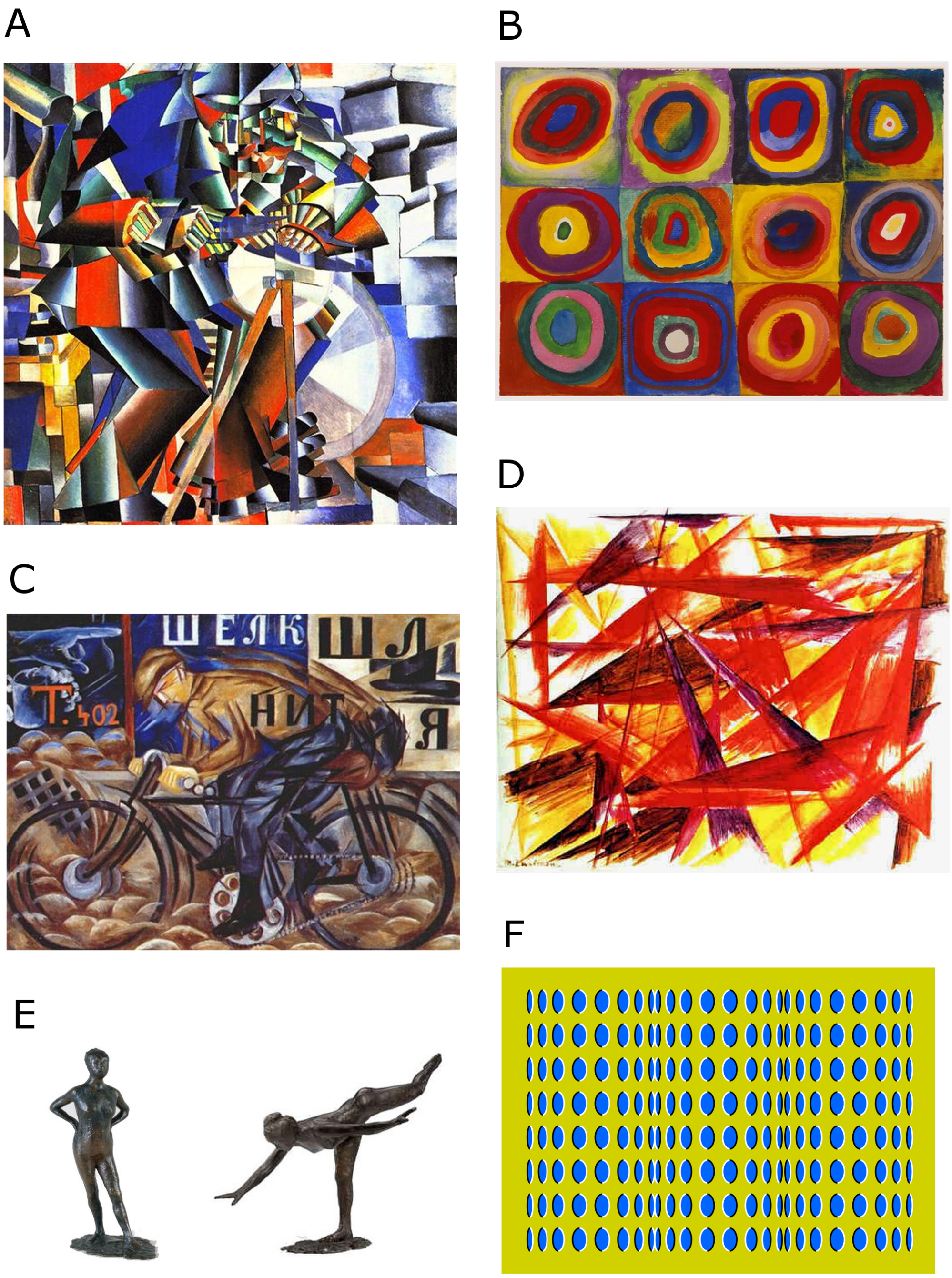

Figure 1. Example of stimuli used in neuroaesthetics experiments. Brain areas encoding movement perception were more activated when expert observers viewed artworks with implied motion such as ‘The Knife Grinder’ by Kazimir Malevich **(A)** than artworks with little implied motion such as ‘Color study - Squares with concentric rings’ by Wassily Kandinsky **(B)** (Kim and Blake, 2007). Applying TMS on brain areas encoding movement perception decreased the sense of movement that naïve observers had in front of paintings, but also their appreciation of abstract artworks such as ‘Red Rayonism’ by Mikhail Larionov **(D)**, but not of representational artworks such as ‘The Cyclist’ by Natalia Goncharova **(C)** (Cattaneo *et al.*, 2015). Greater body sways were observed when participants observed pictures of Edgar Degas’ sculptures of a dancing ballerina (e.g., ‘Grande arabesque, troisième temps’) than of a static ballerina (e.g., ‘Danseuse au repos, mains sur les hanches, jambe gauche en avant’) **(E)** (Nather *et al.*, 2010). Motion illusion was increased when observers spontaneously explored ‘Rollers’ by Akiyoshi Kitaoka **(F**, artwork reprinted with permission, (Kitaoka, 2004)**)** with eye movements than when they fixated the center of the artworks (Kapoula *et al.*, 2015).

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